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**QUANTITATIVE GENETIC ANALYSIS OF
STALK QUALITY CHARACTERISTICS
IN A CORN SYNTHETIC**

BY

MARIA MAGDALENA HELD

A thesis submitted in partial fulfillment
of the requirements for the degree
Master of Science
Major in Agronomy
South Dakota State University
1988

**QUANTITATIVE GENETIC ANALYSIS OF
STALK QUALITY CHARACTERISTICS
IN A CORN SYNTHETIC**

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Date

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MMH

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INTRODUCTION

Considerable progress has been made in improving the standability of corn (Zea mays L.). Further improvement of stalk lodging resistance is still necessary because of increased plant populations and fertilizer inputs. Also, with increased yields and rising drying costs, late season stalk strength will become even more important in the future. Stalk rots are the most important diseases of corn in the U.S. corn belt and associated lodging leads to losses in yield and quality.

The most economical way to minimize losses is to improve stalk lodging resistance. However, lodging is subject to substantial genotype x environment interaction. Stalk quality traits highly correlated with stalk lodging would be helpful in a selection program because they allow the plant breeder to select for stalk lodging resistance independent of the environment.

Progress in any plant breeding program depends on genetic variability in the germplasm and the effectiveness of selection. The breeder is interested in populations with a high mean performance and information on the nature and magnitude of genetic variation present. Knowledge of

genetic correlations among traits is important in plant breeding when two or more traits are concerned. Few genetic studies have been conducted to investigate the relative importance of stalk rot resistance as compared to stalk quality traits and their effects on stalk lodging.

The objectives of this study were: 1) obtain estimates of genetic and phenotypic variances and covariances for stalk quality characteristics, stalk rot resistance, and agronomic traits in SDPP maize synthetic; 2) calculate heritabilities for these traits; 3) investigate genetic and phenotypic correlations between stalk lodging, stalk quality traits, and stalk rot resistance; and 4) examine the suitability of stalk quality characteristics and stalk rot resistance as selection criteria to improve stalk lodging resistance.

LITERATURE REVIEW

Importance of Stalk Lodging

Two types of lodging can be observed in corn production. Root lodging is primarily due to poor brace root development and parenchyma breakdown (31). Only stalk lodging is addressed in this study: a corn plant is considered stalk lodged if the stalk breaks or collapses below the ear. Considerable progress in improving stalk lodging resistance in maize has been achieved during the last four decades. Duvick (18) estimated a 1 % improvement in stalk lodging resistance per year over the last 40 years. Still, 5 to 25 % of potential yield is lost annually due to stalk lodging (75). Losses in yield occur on lodged plants due to poor grain filling and ears are often lost during the mechanical harvest operation. Quality of the grain may be further reduced when the ear of a broken stalk touches the ground and ear rot develops.

Four decades ago, when most of the corn was hand harvested, standability was of less importance to the farmer. Also plant populations have increased steadily over the last 50 years. Because of improved lodging resistance and use of fertilizer, newer hybrids respond favorably to

higher plant populations compared to early hybrids or open pollinated corn (53).

A number of interacting factors cause stalk lodging. Stalk rotting diseases are responsible for stalks breaking at disease-infected nodes. As *Diplodia maydis* resistance was improved in a recurrent selection program in the open pollinated variety Lancaster, stalk lodging decreased (26). Damage by corn borers weakens the stalk and provides entry for stalk rot organisms (6). A high ear and plant height are thought to increase lodging susceptibility in corn. Vera and Crane (68) found a nonsignificant reduction in percent lodging after selecting for lower ear height for two cycles in two populations of maize.

Inherent stalk strength is a major factor in determining stalk lodging resistance. Stalk strength resides principally in the rind tissue (4,5). Cloninger et al. (7) attributed 65 % to the contribution of the rind for crushing strength. Zuber (71) noted a reduction in stalk lodging in a recurrent selection program for high stalk crushing strength.

Soil fertility seems to influence the incidence of stalk lodging. Josephson (27) observed reduced stalk breakage from applications of potash fertilizer. Parenchyma disintegration related with stalk lodging occurs in the

lower portion of the stalk in potassium deficient plants (31).

Importance of Stalk Rot

Stalk rots are the most important diseases of maize in the U. S. Corn Belt and throughout the world. Estimates of yield losses due to stalk rot range from 3 to 20 % (24,39,69). Losses occur because of premature senescence, poorly filled ears and stalk breakage which create harvest difficulties and loss in dry matter production. Stalk rot weakens the stalk and reduces structural strength, resulting in stalk breakage late in the growing season (1).

A variety of organisms are responsible for stalk rots. Anthracnose stalk rot caused by Colletotrichum graminicola (Ces.) G. W. Wils. is most prevalent in the southeastern states and the southern half of the corn belt. Gibberella stalk rot caused by Gibberella zeae (Schw.) Petch. and Fusarium stalk rot caused by Fusarium moniliforme Sheld. show very similar symptoms. This study is mainly concerned with Diplodia stalk rot caused by Diplodia maydis (Berk.) Sacc. (Syn. D. zeae (Schw.) Lev.). The fungus produces flask-shaped pycnidia containing two-celled spores which overwinter mainly on debris and disseminate by rain and wind (58). Infection occurs mainly

through the crown, mesocotyl and roots (30). The disease develops after silking causing pith disintegration and discoloration (58).

Improvement in stalk quality in a recurrent selection program to increase stalk rot resistance has been observed (26). Zuber et al. (72) found that the pith contributes substantially to total stalk crushing strength and therefore stressed the importance of developing strains with *Diplodia* resistance. Foley (19) on the other hand states that thick-walled stems will permit the use of cultivars with less decay resistance.

Soil fertility influences stalk rot severity and a balanced nitrogen/potassium ratio is important. Generally, potassium fertilizer reduces the incidence of stalk rot and nitrogen fertilizer increases the severity of stalk rot (1,27,44,48). Simpson (55) observed less stalk rot without nitrogen fertilization and shallow or no cultivation. His experiments indicate that damage to the corn root encourages the development of stalk rot diseases.

Stalk rot tends to increase with higher plant populations (43). The incidence of stalk rot increased as thinning was delayed: stress from interplant competition elevated stalk rot susceptibility (42). Dodd (16) suggested a photosynthetic stress-translocation balance concept of

the predisposition to stalk rots. The grain sink and stalk are competing for carbohydrates (3) and thereby influencing the rate of senescence which predisposes the stalk to invasion by fungi (16). Barren plants seem to be more resistant to stalk rot (16,45). There is a correlation between declining sugar content in the stalk after silking and stalk rot susceptibility (12). Declining sugar levels were related to senescence of the pith tissue which leads to susceptibility to stalk rot caused by *Diplodia maydis* (13). Pappelis and co-workers (45,46,47) related the spread of pathogens to cell death: living cells in the stalk resist the spread of stalk rotting organisms. Therefore stalk rot ratings were correlated with pith condition ratings (47).

Stalk Quality Characteristics and Correlations Among Traits

The breeder is able to select for stalk lodging resistance only when stalk lodging occurs in the field. Since lodging is greatly influenced by environmental factors, selection is not possible every year. A number of stalk quality traits which are less dependent on the environment have been investigated which are useful for indirect selection. Zuber and Grogan (73) introduced a technique for measuring stalk strength in corn: to

determine stalk crushing strength, 51mm long stalk sections were crushed with a hydraulic press. Selection for stalk crushing strength is an effective method to reduce stalk lodging and identify genotypes with stalk lodging resistance (9,41,71). Selection for high crushing strength in MoSQA and MoSQB maize populations significantly decreased stalk lodging (9).

Rind puncture measurements using a penetrometer were highly correlated with stalk lodging and consistent in distinguishing between lodging resistance levels in hybrids under low and high lodging conditions (63,67). A high correlation with stalk quality make the simple and quick rind strength procedure a valuable selection criteria (37). The rind puncture method measures the contribution of the rind to total stalk strength and allows the completion of one cycle per generation in a cyclic breeding program. Rind puncture values and crushing strength were significantly correlated ($r = 0.81$) at four sampling dates in six single cross hybrids (10). A number of other studies confirm the negative correlation between stalk lodging and rind puncture measurements or stalk crushing strength which were highly correlated with each other (2,65,67).

Lodging resistant plants generally have thicker rinds and stronger stalks than lodging susceptible plants.

(34). Zuber and Loesch (76) outlined how to measure rind thickness with a micrometer. A high correlation between rind thickness and crushing strength exists (35,57,62). It was suggested that rind thickness data might substitute for the more labor intensive crushing strength measurement because of a high correlation of 0.87 (73).

Specific gravity of stem sections can be assessed independent of lodging. It was significantly correlated with stalk lodging, stalk rot ratings, crushing strength, rind thickness and rind puncture rating (64).

Gain from Selection

A significant relationship between physical stalk traits of inbred lines and resistance to stalk lodging in hybrid combinations exists (59). Recurrent selection to increase stalk rind thickness in a synthetic population of maize was associated with a decrease in lodging (14). Zuber (71) successfully upgraded stalk quality with a recurrent selection scheme using stalk crushing strength as the selection criteria. Rind thickness and rind puncture values increased while a slight reduction in stalk lodging was noted.

Jinahyon and Russell (25) achieved significant improvement of stalk rot resistance after three cycles of

recurrent selection in the open pollinated variety Lancaster. They used artificial inoculation with Diplodia maydis and improved stalk rot resistance by 0.7 per cycle on a scale from 1 to 6. Because of mainly additive type gene action the authors concluded that further progress should be possible. Martin and Russell (37) suggested recurrent selection for rind strength and artificial stalk rot resistance simultaneously as a method to improve field quality of populations to be used for inbred development.

Selection for lodging resistance in seven cycles reduced yield significantly although the reduction was minimized in hybrid combinations with unrelated testers (66). Thompson therefore concluded that improvement in lodging resistance should not limit progress for increases in yield. Mass selection was suggested as the most efficient method to improve disease resistance including stalk rot resistance in two populations (40). If an adequate population size was maintained improvement would not affect yield potential. Devey and Russell (15) on the other hand noted an antagonism between high yield and good stalk quality. Substantial yield loss was also observed by Martin and Russell (38) in a recurrent selection scheme for stalk quality in a maize synthetic. The authors therefore suggested to practice mild selection for yield when a population improvement program for stalk quality is

conducted.

Genetics of Maize

Knowledge of the type and magnitude of gene action is important to the plant breeder since it determines the efficiency of a breeding program. Mating designs have been proposed by Comstock and Robinson (11) and used extensively to estimate the kind and relative importance of genetic variation in corn populations. These designs include progenies that involve relationships among relatives having known genetic components of variance. Generally, genetic variability of traits in corn is due largely to additive genetic variance (22,32,51). Sentz (54) estimated genetic variances in a synthetic variety from Design I and II matings. Additive genetic variance was significant and of primary importance for all traits. Dominance variance accounted for 45 % of the genetic variance in yield, but was unimportant for other traits. Additive genetic variance was the major portion of genotypic variance for yield and yield components in the open pollinated variety Reid Yellow Dent (70).

Significant differences among progenies of lodging resistant and susceptible corn inbred lines were found for rind thickness and crushing strength (35). Specific combining ability was of greater importance than general

combining ability in this one year study. In a diallel analysis of 12 inbred lines of corn, additive genetic variation constituted the major proportion of genetic variation for rind thickness, stalk lodging, crushing strength and the large stalk diameter (33). Broad sense heritability estimates for the stalk quality traits were low. Robinson et al. (49) found high heritabilities for ear height whereas yield had lower heritability values.

Stalk rot resistance has been reported to be inherited in a quantitative manner (60). Highly significant differences among inbred lines were observed for stalk rot resistance (52). Additive type of gene action is of greater importance than non-additive for Diplodia stalk rot resistance with medium to high heritability values (25). Generation mean analysis was used by Kappelman et al., (28) to detect types of gene action for Diplodia stalk rot resistance in eight maize populations. Additive gene effects were significant in all populations.

MATERIALS AND METHODS

The South Dakota plant pathology (SDPPS) maize synthetic, synthesized by John Jenison for stalk and root characteristics, was used in this study. A North Carolina Design I mating scheme was employed where fifty plants designated as males were mated to different sets of four female plants each, producing 200 families. Seed of each family was increased by randomly sibbing within each family. The 200 families were grown in 1986 and 1987 in a randomized complete block design with two replications per location.

In 1986, two experiments were planted on May 17 on the SDSU Agronomy Farm near Aurora, SD and on May 20 south of Brookings, SD (Sandpit), respectively. Single row plots of each family were 9.6 and 8.1 m long, spaced 0.9 m apart. Plots were overplanted and thinned, if necessary, to a population of 53,800 plants per hectare to obtain equal plant spacing. In 1987 one experiment was planted on April 28 at the SDSU Plant Pathology Farm and the other experiment on April 29 south of Brookings (Sandpit). At both locations, the single row plots measured 9.6 m in length with rows 0.9 m apart. After thinning, a plant population of 45,200 plants per hectare was obtained. The

soils in experimental plots were classified as an Estelline silt loam (Pachic Udic Haploboroll) at the Agronomy Farm, as a Renshaw sandy loam (Udic Haploboroll) south of Brookings (Sandpit), and as a Vienna silt loam (Udic Haploboroll) at the Plant Pathology Farm.

Experimental plots were fertilized with 100 kg ha^{-1} N, 22 kg ha^{-1} P, and 22 kg ha^{-1} K in the spring except the experiment in Aurora in 1986 which did not receive fertilizer. The corn plots were planted after soybeans at the Agronomy Farm in 1986, sunflowers in at the Plant Pathology Farm in 1987 and after fallow south of Brookings for both years. Tillage consisted of plowing and disking. Chemical weed control was carried out with 0.6 kg ha^{-1} alachlor and 1.1 kg ha^{-1} cyanazine in both locations and years.

Twelve plants per plot at the Agronomy Farm in 1986 and Plant Pathology Farm in 1987 were artificially inoculated with a spore suspension of *Diplodia maydis* (Berk.) Sacc. ($200,000$ spores/ml) one week after flowering. Two ml of the spore suspension were injected into the center of the second internode above the brace roots using a 50 ml Vaco pistol grip syringe. Four weeks later the inoculated plants were cut above the inoculated internode and split to ground level. *Diplodia maydis* reaction was

recorded on 10 plants by the amount of discoloration of the inoculated internode on a scale from 1 to 6:

1 = 0 - 25 %

2 = 26 - 50 %

3 = 51 - 75 %

4 = 76 - 100 %

5 = discoloration beyond inoculated internode

6 = premature death of the plant

Ear height of 10 plants per plot was recorded at the locations mentioned above as the distance from the ground to the ear-bearing node in meters. Rind puncture resistance measurements were made with a rind penetrometer equipped with a Dillon force gauge. The center of the third internode above the brace roots was punctured on 10 plants per plot and the resistance recorded in kg.

Stalk quality characteristics were determined at all locations and in both years on 5 stalks per plot. Stalks were harvested at maturity by cutting at the ground level and at the ear-bearing node. The stalks were air dried and the following stalk traits determined on the second internode or node above the brace roots:

(1) Rind thickness (mm): Measured with micrometer caliper after removal of the pith.

(2) Nodal plate thickness (mm): Measured with a

vernier caliper on split stalks.

(3) Stalk cross-sectional area (mm^2): The major and minor diameter of the stalk were measured, and the cross-sectional area approximated using the formula for the area of an ellipse.

(4) Internode length (mm): Measured with ruler.

Stalk lodging was determined as the percent of stalks broken below the uppermost ear prior to harvest:

$$(\text{number of lodged plants total} / \text{plants per plot}) \times 100$$

The plots were harvested with a plot combine and the grain yield expressed in Mg ha^{-1} at 15.5 % moisture. Grain moisture was determined with a portable grain moisture meter.

A separate analysis of variance was carried out for each experiment and for the years 1986 and 1987. A combined analysis of variance and covariance was carried out as outlined in Table 1. Simple regression analysis was performed for grain yield on the number of plants per plot in all experiments. Grain yield was found to be dependent on plant stand, therefore grain yield was adjusted prior to analysis using the following equation:

$$Y' = Y - b (X - \bar{X})$$

where Y' = adjusted yield; Y = observed yield; b = regression coefficient of yield on stand; and $(X - \bar{X})$ =

TABLE 1 : Form of the analysis of variance and covariance with m males, f females, and r replications in e environments.

Source of variation	Degrees of freedom	Mean squares	Expected mean squares or Expected mean cross products
Total	(rmfe-1)		
Environments	(e-1)		
Reps/E	e(r-1)		
Males	(m-1)	MS5	$\sigma^2_{e_{ij}} + r\sigma^2_{f/mxe_{ij}} + rf\sigma^2_{mxe_{ij}} + ref\sigma^2_{f/m_{ij}} + ref\sigma^2_{m_{ij}}$
Females/males	m(f-1)	MS4	$\sigma^2_{e_{ij}} + r\sigma^2_{f/mxe_{ij}} + re\sigma^2_{f/m_{ij}}$
Males x E	(m-1)(e-1)	MS3	$\sigma^2_{e_{ij}} + r\sigma^2_{f/mxe_{ij}} + rf\sigma^2_{mxe_{ij}}$
Females/males x E	m(f-1)(e-1)	MS2	$\sigma^2_{e_{ij}} + r\sigma^2_{f/mxe_{ij}}$
Error	e(r-1)(mf-1)	MS1	$\sigma^2_{e_{ij}}$

additive genetic variance (i=j) or additive genetic covariance (i≠j) : $\sigma^2_A = 4 \times \sigma^2_{m_{ij}}$

dominance genetic variance (i=j) : $\sigma^2_D = 4 \times (\sigma^2_{f/m_{ij}} - \sigma^2_{m_{ij}})$; and $h^2 = \sigma^2_A / \sigma^2_P$

deviation of number of plants in the plot from the overall average number of plants per plot.

Data from missing plots was estimated by using the value of the alternate replication. One degree of freedom was subtracted for the degrees of freedom for total and error for each missing plot.

The male and female/male mean squares or mean cross products were used to calculate genotypic or phenotypic variances and covariances, respectively. Narrow sense heritabilities were calculated on a family mean basis as the ratio of additive genetic variance to phenotypic variance. Standard errors of additive or dominance genetic variance and heritability were estimated using the formula described by Lothrop et al. (36).

The additive component of covariance for two traits measured in different experiments was estimated by pooled, corrected sums of cross products of observed family means divided by family degrees of freedom. The expected covariance of observed family means due to common environmental effects is zero as noted by Kempthorne (29).

Genetic correlations (r_g) were calculated for all possible combinations of two traits using the following formula:

$$r_g = \sigma^2_{A_{xy}} / \sigma^2_{A_x} \times \sigma^2_{A_y}$$

where $\sigma^2_{A_{xy}}$ = the additive genetic covariance between trait x and y, $\sigma^2_{A_x}$ = estimate of additive genetic variance for trait x, and $\sigma^2_{A_y}$ = estimate of additive genetic variance for trait y.

Phenotypic correlations were calculated similarly using phenotypic covariances and variances. A pooled estimate of genetic and phenotypic covariances was used for traits measured in different environments. Estimates of the variance of genetic correlation coefficients were calculated by the method of Tallis (61), and degrees of freedom estimated as outlined by Gaylor and Hopper (20). Heritabilities and genetic correlation estimates were considered significant if their absolute value exceeded twice their standard error.

Regression analysis to determine the contribution of plant and stalk characters to stalk lodging was carried out. The R-square procedure (SAS, Cary, NC) was used to evaluate the effect of each trait separately, their quadratic responses and all possible interactions between pairs of two traits combined for all locations and years. The five traits giving the highest coefficients of determination, their quadratic form, and their interactions

were used in stepwise (SAS, Cary, NC) regression analysis to select the best model for prediction of stalk lodging.

RESULTS

Means, ranges and coefficients of variation of SDPPS family means (Table 2) demonstrate SDPPS contains large amounts of variability for all traits. The means from both years are in good agreement for rind strength, rind thickness, nodal plate thickness, Diplodia stalk rot score and grain yield. In 1987, ear height was increased whereas internode length was decreased. The larger stalk area in 1987 was probably due to the lower plant population used in that year. Stalk lodging was about twice as high in 1987 as in 1986. The 1987 season was very favorable for the development of a large potential grain sink early in the growing season but moisture stress during grain filling in August probably caused the accelerated translocation of carbohydrates out of the stalk, thereby increasing their susceptibility to stalk rot organisms and subsequent stalk lodging. Grain moisture at harvest was lower in 1987 which can be explained by the earlier planting date and a dry fall.

F-tests of family mean squares were significant at the 0.01 probability level for each trait in the combined analysis of variance (Appendix A). This indicates that genetic variability exists among the families for the

TABLE 2 : Means, ranges and coefficients of variation (CV) of plant and stalk traits of SDPPS families grown in 1986 and 1987.

Trait#	Year 1986			Year 1987		
	Mean	Range	CV	Mean	Range	CV
RST	4.5	3.0 - 6.6	12.4	4.2	3.8 - 4.9	4.6
RT	1.3	1.0 - 1.6	8.2	1.3	1.1 - 1.6	6.4
NT	4.2	3.4 - 5.2	7.5	4.1	3.3 - 5.2	7.7
SA	354.0	250.1 - 496.2	11.4	402.4	297.1 - 575.7	10.1
IL	122.9	101.6 - 147.1	7.8	98.8	72.1 - 122.9	9.3
DIP	3.6	2.1 - 4.6	11.4	3.7	2.2 - 4.9	13.0
EHT	76.9	55.8 - 96.7	9.0	90.5	77.4 - 104.2	5.5
SL	13.6	0 - 38.1	59.6	25.8	6.7 - 55.8	42.1
MST	23.6	19.5 - 30.2	8.2	19.6	16.9 - 22.4	5.4
YLD	5.1	3.0 - 9.1	20.6	5.2	2.7 - 12.5	22.8

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm²), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (cm), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha⁻¹).

traits measured.

Estimates of additive genetic variance were significant for all traits in both years for SDPPS (Appendix B) except rind strength in 1986. Estimates were higher in 1986 for rind strength, rind thickness, internode length, Diplodia stalk rot score, ear height and grain moisture. Environmental variance estimates were higher in 1986 than 1987 for all traits except nodal plate thickness, Diplodia stalk rot score and grain yield. The high estimate of additive genetic variance and low estimate of environmental variance in 1986 resulted in a larger heritability estimate in 1986 than 1987 for Diplodia stalk rot score. Additive genetic and environmental variance estimates for nodal plate thickness increased from 1986 to 1987 resulting in a larger heritability estimate in 1987. Estimates of narrow sense heritabilities were significant when compared to their respective standard errors. However, in 1986 the heritability estimate for rind strength which also showed a nonsignificant additive genetic variance estimate was not significant. In general, heritability estimates of most traits were larger in 1986 than 1987. Ear height and Diplodia stalk rot score showed the highest heritability estimates in both years (Appendix B).

Pooled additive genetic variance and heritability

Table 3 : Pooled estimates of additive genetic variance (σ^2_A), dominance genetic variance (σ^2_D), environmental variance (σ^2_E), and heritability (h^2) of plant and stalk traits in SDPPS.

Trait#	$\sigma^2_A \pm SE$		$\sigma^2_D \pm SE$		σ^2_E	$h^2 \pm SE$
RST	0.0613±	0.0418	0.0739±	0.0555	0.0667	0.30±0.20
RT	0.0084±	0.0027 +	0 *		0.0049	0.63±0.23 +
NT	0.1335±	0.0365 +	0 *		0.0483	0.73±0.20 +
SA	1353.0536±	480.7357 +	342.6864±	604.4960	679.1590	0.57±0.20 +
IL	88.8184±	27.7400 +	0 *		48.2137	0.65±0.20 +
DIP	0.1197±	0.0517 +	0.0057±	0.0742	0.1429	0.45±0.19 +
EHT	0.0039±	0.0013 +	0.0006±	0.0015	0.0028	0.54±0.17 +
SL	85.1636±	27.2861 +	15.8239±	33.3147	33.9123	0.63±0.20 +
MST	3.0452±	0.8739 +	0 *		1.3065	0.70±0.20 +
YLD	1.5279±	0.4361 +	0 *		0.6572	0.70±0.20 +

* Negative estimate assumed to be zero.

+ Heritability or variance estimates differ significantly from zero as its absolute magnitude exceeded twice its standard error.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm²), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha⁻¹).

estimates were significant for all traits in SDPPS except for rind strength (Table 3). The additive genetic variance estimate was exceeded by the dominance genetic variance estimate only in the case of rind strength, although neither of the estimates was significantly different from zero. The environmental variance estimates were larger than the additive genetic variance estimates for all traits except rind strength and Diplodia stalk rot score. However, for none of the traits including rind strength did the dominance genetic variance estimate prove significant when compared with their respective standard errors. Resulting negative estimates for dominance genetic variance for rind thickness, nodal plate thickness, internode length, grain moisture and grain yield were assumed to be zero. Heritability estimates were medium to high for the stalk quality characteristics except rind strength. Estimates of narrow sense heritability were high for grain yield and grain moisture (0.70). Stalk lodging showed a heritability estimate of 0.63 in SDPPS and Diplodia stalk rot score had an intermediate and significant heritability (0.45).

Pooled estimates of genetic correlation coefficients for the traits studied tended to be larger than corresponding estimates of pooled phenotypic correlation coefficients (Table 4). Genetic correlation

Table 4 : Pooled estimates of genetic (above diagonal) and phenotypic (below diagonal) correlation coefficients between plant and stalk traits in SDPPS.

Trait#	RST	RT	NT	SA	IL	DIP	EHT	SL	MST	YLD
-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
RST		0.844*	0.254	0.257	0.212	0.455*	0.205	-0.977*	-0.017	-0.195
RT	0.494		-0.055	0.266	0.015	0.384*	0.400*	-0.585*	-0.226	0.001
NT	0.121	0.044		0.041	0.228	0.045	0.015	0.067	-0.199	-0.005
SA	0.146	0.235	0.110		-0.098	0.463*	0.113	-0.076	-0.089	0.373*
IL	0.153	0.010	0.198	-0.047		0.385	0.300	-0.057	-0.386*	-0.003
DIP	0.063	0.204	-0.020	0.214	0.250		0.589*	-0.081	-0.479*	-0.332
EHT	0.304	0.363	0.020	0.190	0.359	0.244		-0.176	0.034	-0.150
SL	-0.508	-0.460	-0.002	-0.022	-0.078	-0.005	-0.062		0.113	0.128
MST	-0.028	-0.145	-0.137	0.007	-0.274	-0.355	0.076	0.073		-0.051
YLD	-0.050	0.066	-0.030	0.228	0.023	-0.273	-0.080	0.066	-0.043	

* Correlation coefficients differ significantly from zero as its absolute magnitude exceeded twice its standard error.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm²), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha⁻¹).

coefficients judged to be significantly negative or positive were of the same sign and magnitude as the corresponding phenotypic correlation coefficients.

Positive and significant genetic correlations were present between rind thickness and rind strength, ear height and rind thickness, ear height and Diplodia stalk rot score, and stalk cross-sectional area and grain yield. Grain moisture was negatively and significantly correlated with internode length and Diplodia stalk rot score. Diplodia stalk rot score was negatively correlated with grain yield. However, grain yield had no significant correlation with stalk lodging. Rind strength showed a strong significant positive correlation with rind thickness. The five stalk characteristics were genetically positively correlated among themselves with the exception of a small negative correlation between nodal plate thickness and rind thickness, and also internode length and stalk cross-sectional area. Diplodia stalk rot score was positively and significantly correlated with rind strength, rind thickness, stalk cross-sectional area and ear height. Stalk lodging was negatively and significantly correlated with rind strength and rind thickness; no significant correlation between Diplodia stalk rot score and stalk lodging was detected.

Phenotypically, stalk lodging was negatively correlated to all stalk characteristics including stalk rot score. Rind strength was positively phenotypically correlated with rind thickness, but negatively phenotypically correlated with stalk lodging.

Pooled estimates of genetic and phenotypic covariances between the traits studied are shown in Appendix C. In general, phenotypic covariances were greater than genetic covariances in SDPPS. The direction of signs for genetic and phenotypic covariances is reflected in their respective genetic and phenotypic correlation coefficients. Phenotypic covariances between experiments are the same as genetic covariances, since the expected covariances of the observed family means due to common environmental effects are zero. Therefore, the same across-experiment covariance estimates were taken as the phenotypic covariance of two traits measured in different experiments.

Coefficients of determination (R^2) from regression analysis of factors contributing to stalk lodging over all locations and years are presented in Table 5. Rind strength, rind thickness and internode length per se accounted for 15, 12, and 2 percent of the total variation in stalk lodging, respectively. The quadratic response for

TABLE 5 : Coefficients of determination (R^2) from fitting various simple and multiple regression models to explain variation in stalk lodging over all locations and years in SDPPS.

Trait#	R^2		Traits*	R^2
	simple	quadratic		interaction
RST	0.146	0.143	RST*RT	0.185
RT	0.122	0.120	RST*IL	0.120
NT	0.002	0.002	RT*IL	0.113
SA	0.002	0.001	RST*NT	0.089
IL	0.020	0.021	RST*MST	0.082
DIP	0.001	0.002	EHT*RST	0.079
EHT	0.002	0.002	RT*NT	0.076
MST	0.001	0.001	EHT*RT	0.058
YLD	0.000	0.001	RT*MST	0.057
EHT, RST, RT, SA, IL	0.240	0.229		
All traits	0.241	0.237		

* interaction of two traits.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm^2), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha^{-1}).

these traits was very similar. The interaction between rind strength and rind thickness gave the highest R^2 , followed by the interaction of the two traits with internode length. The five traits accounting for the maximum variation in stalk lodging were rind strength, rind thickness, internode length, ear height and stalk cross-sectional area. Addition of the remaining traits into the model did not lead to an increase in R^2 .

Coefficients of determination (R^2) from fitting additional multiple regression models using the five traits selected above, their quadratic forms and all possible interactions are shown in Table 6. The interaction between rind strength and rind thickness resulted in the highest R-square value for a one variable model. Addition of variables lead to only small increases in R-square reaching 0.32 in a ten variable model.

TABLE 6 : The best fitting one to ten variable regression models selected by stepwise regression to predict stalk lodging in SDPPS.

Variables#	R^2
RST*RT	0.19
EHT*SA, RST*RT	0.21
EHT*SA, RST*RT, SA*IL	0.23
EHT*RT, RST*RT, RST*SA, SA*IL	0.23
EHT*RT, EHT*SA, RST*RT, RST*SA, RT*IL	0.24
SA^2 , EHT*RST, EHT*IL, SA*IL, RT, SA	0.29
RT^2 , SA^2 , EHT*RST, EHT*IL, SA*IL, RT, SA	0.30
SA^2 , IL^2 , EHT*RST, EHT*IL, SA*IL, EHT, RT, SA	0.31
SA^2 , IL^2 , EHT*RST, EHT*RT, EHT*IL, SA*IL, EHT, RT, SA	0.32
RST^2 , SA^2 , IL^2 , EHT*RST, EHT*RT, EHT*IL, SA*IL, EHT, RT, SA	0.32

* denotes interaction of two traits.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm^2), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield ($Mg\ ha^{-1}$).

DISCUSSION

The effectiveness of a plant breeding program depends on the existence of genetic variability. Therefore, knowledge of variance components for quantitative traits is necessary for optimal population improvement. The genetic components of variance can be estimated from mating designs under the following assumptions: a) random mating, b) diploid and Mendelian inheritance, c) no environmental correlation among progenies, d) no maternal effects, e) linkage equilibrium, and f) non-inbred relatives (8). The estimates obtained apply specifically to the germplasm pool and environments sampled.

Additive genetic variance was of major importance for the agronomic traits and stalk characteristics, including stalk lodging, in this study. This is in agreement with a number of studies in the literature. (25,32,37,54). Only rind strength had a dominance genetic variance estimate larger than the additive genetic variance estimate, although both estimates were not significantly different from zero. Relatively high additive genetic variance for Diplodia stalk rot score has also been observed by Kapellmann and Thompson (28). In contrast to other research, no dominance genetic variance component

was detected for grain yield (22,54,70).

Heritability determines the progress from selection; characters with high narrow sense heritability can be improved more rapidly than those with lower heritability. Heritability in the narrow sense is the ratio of additive genetic variance to phenotypic variance. Since the heritability estimates of this study were based on a sample of environments (2 years with 2 locations each) the estimates were free of genotype-environment interaction. Still, the estimates apply only to the population and environments sampled.

Narrow sense heritability estimates for all traits were significant with the exception of rind strength. A non-significant additive genetic variance estimate for rind strength led to a low narrow sense heritability estimate. This is in disagreement with Albrecht and Dudley (2) who observed a high heritability for rind strength. All other stalk characteristics showed a medium to high narrow sense heritability estimate (>0.57) which agrees with findings of Sleper and Russell (59). A medium heritability estimate (0.45) for Diplodia stalk rot score was in agreement with findings of Jinahyon and Russell (25). The pooled heritability estimate for ear height was lower than found by Hallauer and Miranda (21), although the estimates for

individual years tended to be higher. A medium to high heritability estimate was observed for stalk lodging (0.63). This result agrees with Sleper and Russell (59) who found a similar heritability estimate for stalk lodging. The high heritability estimate for grain moisture (0.70) is in agreement with results by Hallauer and Miranda (21). The heritability estimate for grain yield was also high. This is consistent with findings by Albrecht and Dudley (2).

Estimates of genetic and phenotypic covariance were pooled across environments since the environmental covariance for two traits measured in different experiments is expected to be zero. There was an almost consistent pattern in the sign of the pooled genetic and phenotypic covariance between stalk quality traits including Diplodia stalk rot resistance and yield components.

Knowledge of genotypic and phenotypic correlations between stalk quality characteristics, stalk rot resistance and stalk lodging/agronomic traits is important as it allows the evaluation of indirect selection for stalk lodging. Pooled estimates of genetic correlation coefficients in this study were generally larger than their corresponding estimates of phenotypic correlation coefficients. This was a result of the estimated genotypic variances being smaller than the corresponding phenotypic

estimates.

Diplodia stalk rot resistance and stalk lodging were not correlated in this study. This is consistent with Zuber et al. (74) who also found no association between stalk lodging and Diplodia stalk rot resistance. Hoffbeck (23), however, found a positive genetic correlation between stalk lodging and Diplodia stalk rot resistance. Our result may point toward the conclusion reached by Albrecht and Dudley (2) who suggested that stalk rot has to reach a threshold to affect lodging. Positive and significant genetic correlations existed between Diplodia stalk rot score and almost all stalk quality characteristics and also ear height. This suggests that vigorous plants tend to be more prone to attack by Diplodia stalk rot organisms (17), although no significant genetic correlation was observed between Diplodia stalk rot score and grain yield in SDPPS. This lack of association was also reported by Miles et al. (40). The genetic correlation between Diplodia stalk rot score and grain moisture was found to be negative and significant. This was expected since Diplodia stalk rot is related to the rate of senescence in the pith (46); later maturing corn lines with higher moisture will have lower Diplodia stalk rot ratings than early maturing lines with low moisture content.

Rind strength and rind thickness were positively significantly genetically correlated with each other (67). No other significant genetic correlation among stalk quality characteristics was detected. Rind strength and rind thickness were negatively and significantly genotypically correlated with stalk lodging. This was expected from a review of the literature (33,57,62,63). The genetic correlations of rind strength or rind thickness and yield components were not significantly different from zero. Singh (56) however had found a high genetic correlation between rind thickness and grain yield. Only stalk cross-sectional area had a positive and significant genetic correlation with grain yield; suggesting that more vigorous plants also yield well. Grain moisture was negatively correlated with stalk quality characteristics. Only in the case of stalk cross-sectional area was this correlation significant. Stalk cross-sectional area and stalk lodging had a very low genetic correlation (4). The genetic correlations between ear height and stalk quality characteristics were positive, although significant only with rind thickness.

Grain yield was positively and significantly correlated only with stalk cross-sectional area. The genetic correlation of grain yield with Diplodia stalk rot score was not significant. This suggests that resistance to

Diplodia stalk rot is inherited independently of yield. No significant genetic correlation between grain yield and stalk lodging was found in SDPPS. This suggests that stalk lodging can be improved in SDPPS without expecting a loss in yield. Albrecht and Dudley (2) and Miles et al (40) had also reported a lack of genetic association between grain yield and stalk lodging. The highly positive correlation between grain yield and ear height detected by Robinson et al. (50) and Lindsey et al. (32) could not be confirmed in this study.

Regression analysis was conducted to identify traits which contribute most to the variability in stalk lodging. Rind strength and rind thickness accounted for 15 and 12 percent of the variability in stalk lodging, respectively. This agrees with findings by Davis and Crane (14) who noted a decrease of stalk lodging after selection for high rind thickness and Martin and Russell (37) who suggested rind strength as a valuable selection criterion for stalk quality. The five traits accounting for maximum variability of stalk lodging and subsequently used in multiple regression were rind strength, rind thickness, stalk cross-sectional area, internode length and ear height. These results suggest that rind puncture strength is more important than stalk rot evaluation; a conclusion which has also been reached by Albrecht and Dudley (2).

Stepwise multiple regression analysis was carried out to come up with a model to predict stalk lodging. The interaction between rind strength and rind thickness gave the highest coefficient of determination of any single variable model (0.19), which did not increase substantially with the addition of variables to the model. The relative low magnitude of coefficients of determination indicates slow progress improving stalk quality thru indirect selection. Albrecht and Russell (2), and Thompson (65) also suggested selection for stalk lodging per se as the most effective method.

In conclusion, heritability estimates will be useful in determining the best method of selection to improve stalk lodging resistance in SDPPS. Genetic correlations among traits are valuable to the plant breeder since they indicate the correlated response that may occur when indirect selection is practiced. They also help identify traits of little importance in a selection program. Unfavorable genetic correlations between traits selected for in a breeding program reduce the gain from selection. Indirect selection is successful when the heritability of the trait selected for is larger than the heritability of the primary trait and the genetic correlation between the traits is substantial. Since none of the stalk quality traits including Diplodia stalk rot

resistance fulfill these criteria and the coefficients of determination from regression analysis are of low magnitude, selection for stalk lodging per se offers the most effective method to improve stalk lodging resistance in SDPPS.

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APPENDICES

APPENDIX A

F-tests of mean squares from combined analyses of variance of plant and stalk traits in SDPPS.

Mean Square#	RST	RT	NT	SA	IL	DIP	EHT	SL	MST	YLD
-----	---	---	---	---	---	---	---	---	---	---
Male	*	**	**	**	**	**	**	**	**	**
Female/Male	**	**	**	**	**	**	**	**	**	**
Male x E	**	NS	NS	**	**	NS	*	**	**	**
Female/Male x E	NS	NS	NS	NS	NS	NS	*	NS	NS	NS

*,** Significantly different from zero at the 0.05 and 0.01 probability level.

NS Not significantly different from zero.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm^2), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha^{-1}).

APPENDIX B

Estimates of additive genetic variance, environmental variance and heritability for plant and stalk traits in SDPPS in 1986 and 1987.

Trait#	Additive genetic variance		Environmental variance		Heritability	
	1986	1987	1986	1987	1986	1987
RST	0.0897	0.0252*	0.2673	0.0486	0.13	0.34*
RT	0.0105*	0.0039*	0.0111	0.0063	0.49*	0.28*
NT	0.1104*	0.1524*	0.0817	0.1000	0.53*	0.60*
SA	1388.6774*	1794.7191*	2187.4179	1157.2290	0.38*	0.48*
IL	116.1468*	72.8758*	88.1550	71.6928	0.57*	0.39*
DIP	0.1696*	0.1542*	0.0677	0.1544	0.72*	0.49*
EHT	0.0063*	0.0032*	0.0011	0.0005	0.66*	0.87*
SL	93.7572*	98.4012*	74.9238	28.5838	0.55*	0.36*
MST	5.6260*	1.4089*	3.6492	1.4319	0.61*	0.50*
YLD	1.7254*	2.2166*	1.0697	3.1389	0.62*	0.41*

* Heritability and additive genetic variance differ significantly from zero as its absolute magnitude exceeded twice its standard error.

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm²), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD = Grain Yield (Mg ha⁻¹).



APPENDIX C

Pooled estimates of genetic (above diagonal) and phenotypic (below diagonal) covariances between traits in SDPPS.

Trait#	RST	RT	NT	SA	IL	DIP	EHT	SL	MST	YLD
RST		0.01909	0.02298	2.34516	0.49544	0.03895	0.00317	-2.23376	-0.00734	-0.05963
RT	0.02555		-0.00183	0.89400	0.04874	0.01213	0.00229	-0.49328	-0.03602	0.01141
NT	0.02311	0.00214		0.54733	0.78591	0.00563	0.00035	0.22621	-0.12674	-0.00228
SA	3.20379	1.32214	2.29150		-34.13598	5.88989	0.25953	-25.92931	-5.73055	16.96149
IL	0.80510	0.01341	0.98975	-27.05733		1.25663	0.17700	-4.96523	-6.34335	-0.03082
DIP	0.01478	0.01215	-0.00437	5.40093	1.51692		0.01274	-0.25947	-0.28909	-0.14194
EHT	0.01165	0.00357	0.00073	0.79016	0.35854	0.01075		-0.10170	0.00372	-0.01157
SL	-2.65359	-0.61517	-0.00884	-12.26466	-10.57729	-0.02866	-0.06088		1.81961	1.45891
MST	-0.02618	-0.03488	-0.12204	0.74173	-6.69245	-0.38368	0.01356	1.77516		-0.11002
YLD	-0.03322	0.01127	-0.01919	16.41413	0.40569	-0.20939	-0.10113	1.13640	-0.13348	

RST = Rind strength (kg), RT = Rind thickness (mm), NT = Nodal plate thickness (mm), SA = Stalk cross-sectional area (mm^2), IL = Internode length (mm), DIP = Diplodia stalk rot measured on a 1 to 6 scale with 1 as most resistant, EHT = Ear height (m), SL = Stalk lodging (%), MST = Grain moisture (%), YLD= Grain Yield (Mg ha^{-1}).

